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INTERSPECIFIC HYBRIDIZATION IN EASTERN ELYMUS

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AMONG the diagnostic features of the genus *Elymus*, the structure of the glumes presents a rather perplexing series of variations. The first part of this paper deals with an analysis of associated stands of *E. Wiegandii* Fern. and *E. riparius* Wiegand in New England that reveals, not only variant forms with unusually indurated and setaceous glumes, but certain morphological and cytological features that are useful in the detection of rare stands of both species in Ontario, Minnesota and Wisconsin, considerably beyond their presently recognized range (Fernald 1950).

Furthermore, in the western Great Lakes area, the exceptional, mid-western representatives of the above eastern species apparently have been easily confused with members of the *E. interruptus* (of recent authors; not Buckley) complex, a series of forms in which the glumes show extensive reduction from a nearly flat to a very setaceous condition. Accordingly, a second part of this paper is devoted to a preliminary study of *E. interruptus* in Minnesota and adjacent areas. Due to a lumping of these taxa with those of more southern range (Chase 1950), however, it is necessary first to present an analysis of *E. interruptus* Buckl. and the related *E. canadensis* L. v. *brachystachys* (Scribn. & Ball) Farwell of Texas. In this complex, an independent development of setaceous glumes has been effected in experimental hybrids, a phenomenon that suggests a parallel to the occurrence of setaceous glumes in northern *E. interruptus*.

It will be shown, however, that to date there appears to be no sound basis for the merger of the two taxa.

E. WIEGANDII × E. RIPARIUS IN NEW ENGLAND

In New England, *E. Wiegandii* and *E. riparius* often grow in the same area along shady, alluvial banks, such as those of the Connecticut River and Lake Champlain drainage systems, where a part of the present study has been focused. Typical *E. Wiegandii* grows in erect clumps, averaging one and a half meters in height and can be identified readily by the pendent appearance of the rather loosely organized spikes that are lax from the time of emergence from the leaf sheaths. Drying and mounting often obscures this distinctive character of the spikes and gives them an arched or flexuous appearance that is common to many variations of *E. canadensis* L. or *E. riparius*. Later development may or may not produce a well exerted condition. In specimens that appear to intergrade, an average palea length of 11–12(15) mm. will serve to separate *E. Wiegandii* from *E. canadensis*, which has an average palea length of (9) 10–11 mm. The thin-textured, relatively wide (1.5–2.0 cm.) leaves of *E. Wiegandii* are equally distinct. Narrow-leaved forms gave rise to more typical wide-leaved plants when the seed was grown in well fertilized and limed soil.

The fact that the glumes of *E. Wiegandii* are commonly rather constricted and indurated at the base hardly ever obscures the striations in this area. On the other hand, the glume bases of *E. riparius* are terete and unstriated, while those of *E. canadensis* are never appreciably indurated but are striated their entire length. Nevertheless, the existence of forms with characters intermediate between those of typical species may be encountered.

In the alder thickets along the banks of Otter Creek in Rutland County, Vermont, a small population of atypical *E. Wiegandii* 2261¹ has been found. The specimens have the usual

¹ All accession numbers without designation refer to the author's specimens on file in the Brown University Herbarium (BRU). Specimens on file elsewhere are indicated by numbers followed by the herbarium abbreviations established by Lanjouw (1939). Specimens raised from seed kindly supplied by Dr. W. G. Dore of Ottawa or Dr. N. C. Fassett of Madison carry these collectors' original numbers and are on file at Brown. The author also wishes to express his appreciation to the curators of the herbaria in the Universities of Minnesota and Wisconsin and the Smithsonian Institution for the loan of specimens.

pendent spikes but are intermediate in other characters between typical *E. Wiegandii* 2263 and *E. riparius* 2262 from the same station, as shown in the following table:—

	E. WIEGANDII		E. RIPARIUS
	2263	2261	2262
Average height	120 cm.	100 cm.	90 cm.
Number of nodes	9	7	6
Middle leaf width	14–18 mm.	10–12 mm.	8–10 mm.
Florets per spikelet	5–6	2–3	2
Glume base	sl. indurate, striate	indurate, rarely striate	indurate, non-striate
Palea length in basal floret	11.5–12 mm.	10–10.5 mm.	7–7.5 mm.
Shrivelled pollen	40%	80–100%	10%

Although there is some genetical imbalance noted in all populations, it would seem as though the very high pollen sterility in 2261 is correlated with the intermediate characters and indicates a probable hybrid origin. The determination of the precise path of hybridity is by no means easy, however, since other species available for intercrossing include the common *E. virginicus* L. and the less frequent *E. canadensis* of the same area. The rarity of the latter species at this station seems to be explained by its preference for more open terrain.

An experimental program, aimed at learning something of the interrelationships of the eastern species of *Elymus* through the production of interspecific hybrids has been in progress for three years. Hybrids, with varying degrees of success, have been obtained between all four of the above mentioned species. In most cases, the F_1 is completely sterile and attempts at back crossing have met with failure. In a few instances, however, F_2 's have been obtained from a very meager seed set in the F_1 . Bagging experiments have indicated that selfing does not cut down more than 10–20 per cent on seed setting in the parental forms. Furthermore, anthers are found frequently in a shedding state completely inside the florets as the caryopsis develops, a fact which again indicates selfing. Since all of the species of *Elymus* concerned are tetraploid ($2n = 28$), it is reasonable to suppose that many genes are present in quadruplicate and that a certain amount of heterozygosity would not result in complete sterility. As a matter of fact, very few of the hybrids obtained show a lack of affinity between more than

three or four pairs of chromosomes out of a total of fourteen pairs in the pollen mother cells. In other words, *E. Wiegandii*, *riparius*, *virginicus* and *canadensis* have at least one genome and varying parts of another in common. This conclusion is based on the results of crosses of parental forms both adjacent and widely separated in the range. It is difficult, therefore, to determine a precise pattern of interrelationship.

Attempts at crossing *E. Wiegandii* and *E. riparius* were particularly successful in producing hybrids approaching the natural intermediate 2261, however, when pistillate *E. Wiegandii* 2216, from the banks of the West River in Windham County, Vermont, was pollinated with *E. riparius* 2249 from thickets along the Winooski River to the north in Chittenden County. Several dozen seedlings were obtained, two thirds of which possessed a heavy anthocyan pigmentation and eventually died. The surviving green forms have narrow leaves, two florets per spikelet, paleas averaging 8.5 mm. in length and glumes strongly indurated at the base. Spikes are typically pendent. Although one plant is still alive, all maturing offspring are sterile. The reciprocals resemble *E. riparius* very closely but were quite late in producing spikes. In fact, several plants never developed beyond the vegetative stage. It is evident, then, that *E. Wiegandii* and *E. riparius* may give rise to hybrid populations, although no F_2 's or backcrosses have been obtained.

In *E. Wiegandii* 2263 from Otter Creek, however, an apparently unique chromosome behavior was observed in the course of making the preliminary cytological survey for the hybridization program (Vilkomerson 1950). An examination of material from many other stations to date has revealed one or two and often six or seven pairs of chromosomes with their ends prematurely directed toward the poles in the first and sometimes the second meiotic divisions. Variation in the number of pairs involved has been noted particularly in strains from Windham County, Vermont 2216, Franklin County, Mass. 2200, and Coos County, N. H. 2226. In some of the above cases, the points of spindle fiber attachment appear subterminal as well as terminal. In all instances, the attachment points that are distal to the usual median or near median position are termed neocentromeres.

As would be expected in the case of the highly sterile strain 2261 from Otter Creek, varying degrees of lagging chromosomes, bridges and rings at anaphase, and micronuclei in the quartets were found in many, though not all, of the pollen mother cells. The characteristic neocentric pairs of chromosomes were always present in addition to the configurations due to hybridity.

In the light of the above discovery, it was suspected that the neocentric chromosomes could be used as a cytological marker to identify the presence of the "Wiegandii genome" in hybrids in which this species was employed as the staminate parent. This assumption was demonstrated to be correct, not only in crosses with *E. riparius*, but with *E. canadensis* or *E. virginicus* employed in each case as the pistillate parent.

E. WIEGANDII AND E. RIPARIUS IN THE GREAT LAKES AREA

When a study of *Elymus* in the Minnesota area was begun, the cytological marker proved to be very useful as an aid in the identification of strains of *E. Wiegandii* that appear to intergrade with other species or occur considerably beyond their present recognized range. The test was first applied to material from Fort Francis in the Rainy Lake area of southwestern Ontario, at the Minnesota border, where it was found growing close to typical *E. canadensis*. The collector, Dr. W. G. Dore of the Canadian Department of Agriculture, identified it as *E. interruptus* Buckl., Dore 9175 OTB., and very kindly sent herbarium specimens and seeds to the writer. The plants grown in the greenhouse as well as those in the outdoor plots at Brown University have pendent spikes, leaves 10–12 mm. wide, glume bases indurate and usually striate, four florets per spikelet, and paleas 9.5–10 mm. long. Neocentric chromosomes appear consistently at meiosis and hence it is evident that the Fort Francis stand is *E. Wiegandii*. Its presence along the Canadian border, nearly a thousand miles west of the range as stated in Gray's Manual, is supported by another rare occurrence in Cook County, Minnesota, reported by Butters and Abbe (1953).

A cross of *E. Wiegandii*, Dore 9175, and *E. virginicus*, Muligan & Forsyth 282 OTB., from Carleton County, Ontario, revealed the same inheritance of neocentric chromosomes as in crosses involving eastern strains.

Specimens of "atypical canadensis" collected by Dr. N. C. Fassett, 28971-72 WIS., in northwestern Grant County, Wisconsin, yielded seeds that gave rise to typical *E. Wiegandii*, including characteristic neocentric chromosomes, in the Brown University plot. As far as herbarium specimens indicate, this species apparently occurs also in Chippewa County, Davis, no number WIS., and Eau Claire County, Kunz 356 WIS.

Although the distinct features of *E. Wiegandii* were clearly delineated by Fernald (1933), it is not recognized in the Manual of Grasses (Chase 1950). With material at their disposal, Booher and Tryon (1948) could not separate this species from *E. canadensis* in Minnesota. In view of the above evidence, however, the occurrence of *E. Wiegandii* in both Minnesota and Wisconsin seems definitely established.

E. riparius, like *E. Wiegandii*, is also a rare species in the western part of the Great Lakes area. It is not listed from Minnesota by Booher and Tryon (1948), although a few scattered stations occur in Wisconsin (Fassett 1951) in addition to one in northern Illinois (Steyermark 1953). Eastward from Indiana (Deam 1940), it is rather frequent.

Apparently the first record of *E. riparius* in Minnesota is the writer's collection in Nerstrand Woods, Rice County, 2362-66. These specimens have uniformly narrow, indurated glume bases, paleas 7.5-8.0 mm. long, and straight awns, as in the eastern representatives. The habitat is the frequently overflooded banks of a shallow brook in a mixed woodland. The writer has identified an equally rare stand on steep, wooded, limestone cliffs in Grant County, southwestern Wisconsin, 2370.

The fact that these scattered, outpost stations of both *E. Wiegandii* and *E. riparius* have been overlooked in the western part of the Great Lakes area until recently is due probably to their being identified as part of the widespread series of forms with setaceous and often reduced awns in central and northern Minnesota, as mentioned earlier. This series has been interpreted as *E. interruptus* Buckl. in the Manual of Grasses (Chase 1950), a treatment which is followed in the eighth edition of Gray's Manual (Fernald 1950). A comparative study of specimens from both Texas and Minnesota, however, will indicate the lack of affinity between these two taxa and the need for a further inquiry into their relationships.

THE *E. INTERRUPTUS*-*CANADENSIS* COMPLEX IN TEXAS

The type locality of *E. interruptus* (Buckley 1862) is Llano County, Texas. Seed collected in this area, through the kindness of Dr. W. V. Brown of the University of Texas, has produced a series of populations, all of which appear as variations within or closely allied to the *E. canadensis* complex in the state. These forms are quite distinct from all the northern representatives of *E. canadensis* growing at Providence in their earlier attainment of anthesis of a month to six weeks. They are usually shorter and the awns are not reflexed, even at maturity.

E. canadensis L. v. *brachystachys* (Scribn. & Ball) Farwell is represented by several strains, 1026-29, which average about 80 cm. in height and have spikes 10 cm. long. Glumes may be more or less indurated at the base and vary in width from 0.5-1.0 mm., with the widest part in the middle of the length. Strains have been selected which have lemmas that are glabrous, glaucous or hirsute. There is also frequent though inconstant occurrence of three instead of the usual two spikelets per node. A seed collection from a station near Palo Duro Canyon in Randall County, over 400 miles northwest in the Panhandle, gave rise to plants that do not differ from Llano County material except in the glumes, which are flat and striate at the base and have a width of 1.0-1.5 mm. There arose from this population, however, a strain 1030, that differs from all others in reaching often 1.5 m. in height, 25 cm. in length of spike and having always three spikelets per node. The glumes average 1.8 mm. in width. Except for the much earlier time of anthesis, there is a general resemblance to vigorous northern forms. Crosses between late blooming individuals of 1030 and northern *E. canadensis* were a failure, however.

E. interruptus Buckl. is represented in the Llano County populations by a strain, 1040, that has the appearance of a small form of *E. canadensis* v. *brachystachys* in averaging 60 cm. in height. It is reasonably distinct also in the longer distance of 0.9-1.0 cm. between nodes on the spike and the narrow (0.2 mm.), essentially setaceous glumes. Except for the glaucous lemmas, 1040 does not differ materially from cotype specimens of *E. Pringlei* Scribn. & Merr., 731015 US., from Hidalgo, Mexico. Furthermore, Llano County specimens of *E. inter-*

ruptus, 1019510 US., that bear the notation "identical with type" and have glumes 0.5 mm. wide, are intermediate in this feature between *E. interruptus* 1040 and *E. canadensis* v. *brachystachys* 1026-29. As far as general habit is concerned, all of these southern taxa appear to belong to a single species complex.

Another seed collection of *E. interruptus*, 1041, from a station along the Pedernales River, some 50 miles south of the Llano County stand, gave rise to plants that exhibited considerable variation from glabrous to glaucous or hirsute lemmas and from 0.3-0.9 mm. in width of glumes. Furthermore, the glumes are without any bulge in the center as in *E. canadensis* v. *brachystachys*. When spikes exhibiting five different combinations of the above characters were bagged, only 6-10 per cent seed was set. An exceptional strain with glabrous lemmas and glumes 0.7-1.0 mm. in width yielded 22 per cent seed. (For calculation purposes, two seeds per spikelet is considered a normal yield.) Only this latter strain continued vigorous growth for three years. It appears, then, that the variability and vigor of the original population 1041 is maintained, in marked degree, by the interbreeding of its members.

HYBRIDS OF HYSTRIX WITH THE *E. INTERRUPTUS*-*CANADENSIS* COMPLEX

In view of the fact that Booher and Tryon (1948) have implied that the setaceous type of glume in populations of so-called *E. interruptus* in Minnesota has arisen through the natural crossing of *E. canadensis* and the usually glumeless genus *Hystrix*, the writer attempted some breeding experiments to test such a hypothesis for the origin of *E. interruptus* in Texas. A survey of all the strains of *E. interruptus* or *E. canadensis* v. *brachystachys* under study has revealed no meiotic irregularity or significant pollen sterility.

Since the range of *Hystrix* does not quite reach Texas, it was decided to use material available in Providence County, Rhode Island, which is *H. patula* Moench v. *Bigeloviana* (Fern.) Deam, 2302. This northern variety is useful in crossing experiments since the pubescence of the lemmas is readily transmitted through the staminate parent. The glaucous lemmas and wide

(1 mm. at center) glumes with indurated and striated bases of strain 1029 of *E. canadensis* v. *brachystachys* furnished ideal contrasting characters in the pistillate parent. Seed set in the cross was fairly high at 19 per cent. The F_1 inherits the spreading condition of the mature spikelets as well as the pubescence of the lemmas of *Hystrix*. The glumes are very setaceous and irregular in length. The few surviving plants are completely sterile. Reciprocal crosses were failures.

More successful was a cross in which selected plants of *E. interruptus* 1041 were pollinated with *Hystrix* 2302. Half of the F_1 has slightly hirtellous lemmas and the glumes are setaceous and occasionally reduced to stubs. These plants yielded 8 per cent seed. The other half of the F_1 has glumes 0.3–0.5 mm. wide and the seed set was 50 per cent. All of the F_2 plants are vigorous and have glumes in the same width range of 0.3–0.5 mm. It would appear, then, that a population has been formed in which the glumes are not setaceous as in the more typical *E. interruptus* 1040, but through the acquisition of some genes from *Hystrix*, are narrower on the average than the glumes of parental *E. interruptus* 1041. Attempts at crossing typical *E. interruptus* 1040 and *Hystrix* 2302, however, met with failure.

No hybrids were obtained between the vigorous *E. canadensis* v. *brachystachys* 1030 and *Hystrix* 2302. In a cross of pistillate *Hystrix* 2301 from Maryland with *Elymus* 1030, a few plants were obtained with rather distorted spikes, all of which exhibited a great variety of glumes from those 0.5 mm. wide down to minute bristles. Examination of young anthers revealed several lagging univalent chromosomes at meiosis and much shrivelled pollen.

Although it is possible to hybridize *Hystrix* and members of the *E. canadensis*—*interruptus* complex in Texas, it appears that the cross is made with difficulty. Progeny with very setaceous glumes obtained so far have been sterile. It is conceivable, however, that populations of *E. interruptus*, with narrow but not quite setaceous glumes as in 1041, represent forms that have been established after backcrossing of *Elymus-Hystrix* hybrids to either parent.

The question next arises whether or not setaceous or even reduced glumes could appear in the progeny resulting from

crosses within the *E. canadensis*—*interruptus* complex but not directly involving *Hystrix*. Typical *E. canadensis* v. *brachystachys* 1028 was crossed with both strains of *E. interruptus*. Only those crosses with *E. canadensis* as the pistillate parent produced any seed. Out of a total of 400 florets, 14 rather shrivelled seeds were obtained. Two plants from the cross involving 1041 as the staminate parent survived and these have flat glumes.

In striking contrast to the very low degree of affinity between the above strains is the success of the cross between the vigorous, wide-glumed strain 1030 of *E. canadensis* v. *brachystachys* and staminate *E. interruptus* 1040 with narrow to setaceous glumes. Although many seeds were shrivelled, 53 were formed in 65 florets. From a progeny of 26 seedlings, 20 vigorous plants matured, all with flat glumes, but much narrower (0.5–1.0 mm.) than those of the pistillate parent (1.0–1.5 mm.). Sterility ran high, but 7 seeds were obtained from 730 florets. The F_2 was composed of plants equally as vigorous as the F_1 but possessing setaceous glumes of irregular length. The reciprocal cross produced an F_1 more intermediate in glume width although completely sterile. Unfortunately, the F_2 setaceous segregates are also sterile.

To what extent the above experiments indicate that *E. interruptus* Buckl. in Texas is a product of a series of crosses between *E. canadensis* v. *brachystachys* and some strain of *Hystrix*, it is difficult to state. Most crosses reach a sterility barrier in the first generation. Since there are no outstanding meiotic irregularities involved, the barrier consists of relatively few genes. It is of particular significance to note further that populations of *Elymus* with reduced glumes may arise independently of *Hystrix* as a direct parent and that the degree of reduction to setae, as in the cross of 1030 and 1040, exceeds anything yet observed in Texas plants. In fact, the glumes of this hybrid population are similar to those that are encountered in so-called *E. interruptus* of Minnesota. The similarity is due to a case of parallel development, however, since the northern and southern taxa appear to the author to be unrelated if the wide differences in time of bloom and habit of growth as well as genetic barriers are considered.

E. INTERRUPTUS IN MINNESOTA

In a survey of *E. interruptus* in the North, one is impressed by the similarity of plants from Wyoming and the Dakotas to those plants with very reduced glumes in northern Minnesota. Representatives from the type locality of *E. diversiglumis* (Scribner and Ball 1900) in Crook County of northeastern Wyoming, 1019960, 64973 US., or from Bottineau County, North Dakota, 1019513 US., are definitely part of the Minnesota complex. In fact, collections from Pembina County, North Dakota, 253470 MIN., adjacent to the Minnesota border, exhibit a reduction of many of the glumes from setae to mere stubs. Such extreme forms are found not infrequently as scattered individuals in the moist, mixed hardwood forests of north central Minnesota.

As Booher and Tryon (1948) have shown, specimens may be encountered with very narrow but not completely setaceous glumes which appear to grade directly into forms of *E. canadensis*. The writer found this relationship to be true particularly in mixed populations bordering the western edge of Mille Lacs Lake in east central Minnesota. Plants with glumes more than 0.5 mm. wide and paleas over one cm. long appear to be inseparable from robust forms of *E. canadensis*. Until more information about the relationships of the latter species is available, however, it seems desirable to continue to refer to the populations with very narrow or setaceous glumes in the Great Lakes area as *E. interruptus* of recent authors but not Buckley.

Seed collections from forty clones were made in the fall of 1951 from Mille Lacs, Aitken, Crow Wing, Hubbard, Clearwater, Becker and Ottertail Counties in Minnesota. The progeny are represented by apparently healthy plants in the Brown University experimental plots, but to date only half of these have produced spikes. All types of glumes from setaceous to very reduced are represented. Palea length, a character that has proven reliable in separating many species, overlaps that of *E. canadensis*. Although the evidence at hand indicates that each form breeds true, yet several clones which arose from spikes showing great variation in glume structure still remain in a vegetative condition. No meiotic irregularities or appreciable pollen sterility have been noted in any of the plants

examined. By way of contrast, it is noteworthy that many apparently stable forms of *E. canadensis* in the Connecticut River Valley of New England reveal meiotic irregularities in about 5 per cent of the pollen mother cells.

Attempts at crossing *E. canadensis* and *Hystrix patula* from northern areas in the hope of obtaining progeny with setaceous glumes have met with failure thus far. One certain barrier to natural crossing of these two genera is the fact that *Hystrix* comes to anthesis four to six weeks earlier. Furthermore, an examination of specimens from many parts of the range will reveal the fact that although this latter genus is usually characterized by a complete lack of glumes, occasionally stubs or even setae of varying length may occur. Plants from Rice County, Minnesota, 2368, have setae of varying length at every node of the spikes, but are typical in every other character. The station is roughly 100 miles from any stand of *E. interruptus* known to the writer. Specimens from Davidson County, Tennessee, 1021371-2, 1161614 US., also exhibit glume variations from long setae to stubs. The herbarium sheet record indicates that these specimens have at one time been identified as *E. interruptus*, but the present writer feels that they are definitely forms of *Hystrix patula*. Incidentally, this elimination of Tennessee from the distribution map of *E. interruptus* as published in the Manual of Grasses (Chase 1950) will show a clearer geographic separation of the northern and southern taxa, in support of other data presented earlier on this point.

It is significant, then, that *Hystrix* with variable glumes may exist many miles away from stands of *Elymus*. In contrast, *Hystrix patula*, 2306, from a stand adjacent to that of *E. interruptus*, 2305, along the north boundary of Itasca Park, Minnesota, is consistently lacking in glumes. If *Hystrix* is studied from its entire range, it can be deduced that the unusual occurrence of setaceous glumes is a variation not necessarily linked to hybridization with *Elymus*. Indeed, the writer's data showing the early failure of seedlings in hybrids between *Hystrix patula* and both *E. canadensis* and *E. virginicus* from northern populations would seem to indicate the presence of strong genetic barriers between these two genera, although probably only slightly greater than barriers between some species of *Elymus* per se.

The problem of the origin of *E. interruptus* in Minnesota is not simple, as the above attempts at solution indicate. The continuing genetic analysis of the clones available to the writer may still yield information concerning a connection with *Hystrix*. It seems equally possible, however, that gene combinations controlling increased induration and setaceousness of the glumes can arise in populations of *Elymus* not in contact with *Hystrix* at all. Such is the case, at least, in the previously mentioned instance of *E. Wiegandii* and *E. riparius* in Vermont and of *E. canadensis* 1030 and *E. interruptus* 1040 in Texas.

All of the eastern species of *Elymus*, except *E. villosus* Muhl., have been found to produce interspecific hybrids with varying degrees of success. It is quite possible, therefore, that the "gene pool" of *Elymus* may be tapped by chance through several different paths of interspecific hybridization to bring about reduction of the glumes, as the foregoing experiments indicate.

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